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Bateman, A W ; Ozgul, A ; Nielsen, J F ; Coulson, T ; Clutton-Brock, T H

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Social structure mediates environmental effects on group size in an obligate cooperative breeder, *Suricata suricatta*

A. W. Bateman,[1,5] A. Ozgul,[1,2] J. F. Nielsen,[3,4] T. Coulson,[2] and T. H. Clutton-Brock[1]

[1]*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ United Kingdom*
[2]*Department of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY United Kingdom*
[3]*Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT United Kingdom*
[4]*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY United Kingdom*

Abstract. Population dynamics in group-living species can be strongly affected both by features of sociality per se and by resultant population structure. To develop a mechanistic understanding of population dynamics in highly social species we need to investigate how processes within groups, processes linking groups, and external drivers act and interact to produce observed patterns. We model social group dynamics in cooperatively breeding meerkats, *Suricata suricatta*, paying attention to local demographic as well as dispersal processes. We use generalized additive models to describe the influence of group size, population density, and environmental conditions on demographic rates for each sex and stage, and we combine these models into predictive and individual-based simulation models of group dynamics. Short-term predictions of expected group size and simulated group trajectories over the longer term agree well with observations. Group dynamics are characterized by slow increases during the breeding season and relatively sharp declines during the pre-breeding season, particularly after dry years. We examine the demographic mechanisms responsible for environmental dependence. While individuals appear more prone to emigrate after dry years, seasons of low rainfall also cause reductions in reproductive output that produce adult-biased age distributions in the following dispersal season. Adult subordinates are much more likely to disperse or be evicted than immature individuals, and demographic structure thus contributes to crashes in group size. Our results demonstrate the role of social structure in characterizing a population's response to environmental variation. We discuss the implications of our findings for the population dynamics of cooperative breeders and population dynamics generally.

Key words: demographic decomposition; environmental stochasticity; generalized additive model, GAM; group dynamics; local dynamics; meerkats; Monte Carlo simulation; Northern Cape, South Africa; obligate cooperative breeders; population dynamics; social species; stage structure; Suricata suricatta.

Introduction

Population dynamics of social, group-living species can differ markedly from those of solitary species comprising relatively homogeneous populations. Social structure per se can have dynamical consequences, such as thresholds for successful emigration or group persistence (Courchamp et al. 1999, Packer et al. 2005), and group living also implies spatial structure, with associated complications relating to dispersal, regional synchrony, and population persistence (e.g., Hanski 1999). Although such structure does not guarantee atypical dynamics (Frank and Brickman 2000, Bateman et al. 2011*a*), the potential needs to be considered when examining the population dynamics of social species. Local processes, such as social interactions; broad-scale processes, such as dispersal; and external drivers, such as environmental conditions, can all play a role (Bjørnstad et al. 1999, Packer et al. 2005, Ozgul et al. 2009). To develop a mechanistic understanding of dynamics in a given population, we must ask how these processes act and interact to produce broader patterns.

Whereas studies of uniform populations can afford to focus, implicitly or explicitly, on changing population-wide rates of birth and death (e.g., Coulson et al. 2008), studies of socially structured populations must also consider local (group-level) dynamics and dispersal processes. Even the simplest metapopulation models reveal the potential importance of dispersal among habitat patches (Hanski 1999), and recent work has highlighted the important role that local dynamics play in the overall dynamics of group-living species (Packer et al. 2005, Ozgul et al. 2009).

Group dynamics and dispersal are, in fact, closely related. We can describe dispersal in three phases: emigration, transience, and immigration, of which two

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[5] E-mail: awb42@cam.ac.uk

(emigration and immigration) are directly tied to groups where individuals must weigh information relating to resource availability, survival prospects, and reproductive potential (Bowler and Benton 2005). Immigration and emigration directly contribute to dynamics within groups, and within-group processes likely play a particularly important role in the dispersal of social species. Group conditions, through their influence on the costs and benefits associated with remaining in or leaving any group, are major determinants of dispersal—when and how individuals emigrate from their natal group and where, or if, they join a new group are affected by the social environments within those groups (Bowler and Benton 2005, Clutton Brock and Lukas 2011). Changes in group composition alter the social landscape, and thus the incentives surrounding dispersal. One sex is often philopatric, remaining in the natal group to breed, while the other sex emigrates to seek mating opportunities elsewhere (Clutton Brock and Lukas 2011), but the presence of kin may lead to kin competition or inclusive fitness benefits that select for or against different dispersal strategies in different situations (Bowler and Benton 2005).

Linked by emigration and subsequent immigration, or group formation, group dynamics combine to produce population dynamics. Thus, if we aim to understand what drives population-level patterns, we must first understand group-level patterns. Within groups, how do intrinsic demographic processes combine and interact with extrinsic drivers, such as fluctuations in environmental conditions, to produce group dynamics? Relative to other demographic rates, how does dispersal contribute to group dynamics, and how do group dynamics, in turn, affect dispersal? How do social structure and social interactions influence these processes?

Here we report a detailed investigation of group dynamics in highly social meerkats, *Suricata suricatta*. Meerkats provide an excellent system in which to investigate social group dynamics: they are well-studied behaviorally, and detailed life-history data, at fine temporal resolution, exist for multiple groups over more than a decade of field study in a wild population. We use these data to construct an empirical model, with the aim of better understanding meerkats' group-level demography, the patterns of emigration and immigration linking groups, and how these processes influence each other and are influenced by highly stochastic environmental conditions.

Past work has shown that dispersal plays an important role in regulating meerkat group size and that sharp declines after dry years result from increased rates of emigration (Bateman et al. 2011*b*). It remains unclear, however, whether elevated rates of apparent emigration are due to an effect on per capita rates after dry years (potentially including biases in detection, e.g., undetected mortality, which mimics emigration, resulting from reduced body condition) or whether they result from shifts in the age structure of groups (Bateman et al. 2011*b*). The model we describe here has been motivated in part by these observations.

Our model is spatially implicit, considering groups in a descriptive context of environmental and population conditions, and demographically explicit, modeling mortality, recruitment, immigration, and emigration in two-month timesteps as functions of intrinsic and extrinsic predictors. We treat different sex classes, age classes, and dominance classes separately, allowing for different patterns in each component demographic rate. By incorporating finer temporal and demographic structure than used in previous models, we show how different processes are related seasonally and over the course of our study, and clarify the relationships among environment, dispersal, and demographic structure in this social species. Specifically, we investigate the causes of declines in group size after dry years, assessing the contributions of elevated emigration rates per se and those that result from shifts in age structure within groups.

Study Species

Meerkats are arid-adapted social mongooses native to southern Africa. Living at approximate population densities of 7–17 individuals/km^2 (Bateman et al. 2011*a*), they form groups of up to 50 individuals. Seasonal rainfall strongly affects the regional ecology and thereby meerkat reproduction, survival, and overall population dynamics (Clutton-Brock et al. 1999*a*, Bateman et al. 2011*a*). Long-term rainfall (over the previous nine to ten months) is also a good predictor of meerkat body condition (English et al. 2011).

Dispersal shapes meerkat social structure and group dynamics. Females are considered philopatric, but in each social group a long-lived dominant pair produces the majority of offspring (Clutton-Brock et al. 2008, Sharp and Clutton-Brock 2010), and the dominant female, when pregnant, often evicts subordinate females—sometimes permanently—to suppress their reproduction and avoid infanticide (Clutton-Brock et al. 1998, 2008). Subordinate males engage in reproductive prospecting forays, and occasionally form "roving coalitions" that can seize dominance at other groups, often displacing resident males, or form new groups with unrelated female evictees (Doolan and Macdonald 1996, Young 2003). As obligate cooperative breeders, subordinates of both sexes nonetheless assist in raising the closely related dominants' dependent offspring, thus accruing inclusive fitness benefits (Doolan and Macdonald 1996, Clutton-Brock et al. 1999*b*). Although dispersal may lead to direct fitness benefits, the individual risks are high (Stephens et al. 2005), and it reduces group size and thereby the survival prospects of nondispersing kin (Clutton-Brock et al. 1999*a*, Bateman et al. 2011*b*).

Dominant females come into oestrus soon after giving birth and produce multiple litters, usually of one to seven pups, per year (Hodge et al. 2008). The breeding

season peaks in January, to coincide with seasonal rains, and reaches a low in July (Clutton-Brock et al. 1999*b*). Gestation lasts for about 70 days (Young et al. 2006). Pups remain at the natal burrow for about 25 days after birth, attended by one or more older individuals while the rest of the group forages (Clutton-Brock et al. 2002). Females suckle pups for up to two months, but pups are nutritionally dependent on other group members until almost three months of age (Clutton-Brock et al. 1999*b*, 2002). Individuals contribute little to cooperative activities until about six months, and are not sexually mature until about a year (Clutton-Brock et al. 2002).

As might be expected in the semi-arid regions of southern Africa, seasonal rainfall has a strong effect on meerkat population and group dynamics (Clutton-Brock et al. 1999*a*, Bateman et al. 2011*a*, *b*), a relationship that, at the group level, appears to be mediated largely by environment-dependent dispersal (Bateman et al. 2011*b*). Annual emigration rates increase markedly in large groups after years of low rainfall, but the mechanism remains unclear; individuals may fail to return from eviction or prospecting when they are in poor physical condition, or group composition may become biased towards mature individuals ready to disperse in the year after a poor reproductive season (Bateman et al. 2011*b*). Rainfall also appears to affect reproduction, reportedly by increasing the frequency of breeding and rate of pup survival rather than the size of litters (Doolan and Macdonald 1997, Clutton-Brock et al. 1999*b*, Hodge et al. 2008).

Group- and population-level density dependence affect meerkat demography (Clutton-Brock et al. 1999*a*, 2008, Hodge et al. 2008, Bateman et al. 2011*a*, *b*). Evidence suggests that annual population-level dynamics, at least, are affected by population density (Bateman et al. 2011*a*), and group size has an effect on group-level dynamics as well as many life-history traits, including recruitment, survival, and dispersal rates (Clutton-Brock et al. 1999*a*, 2008, Hodge et al. 2008, Bateman et al. 2011*b*).

Methods

Data collection

We used individual-based demographic data from a population of habituated, wild meerkats on and near the Kuruman River Reserve (26°58′ S, 21°49′ E), an area of ranchland near Van Zylsrus in the Northern Cape province of South Africa. Details pertaining to the site are available elsewhere (e.g., Clutton-Brock et al. 1999*a*). During weekly (and often daily) visits to meerkat social groups between January 1998 and December 2008, researchers collected detailed life-history records for individually marked meerkats (Clutton-Brock et al. 1998, 2008). These records detailed group composition and individual reproduction (including pup birth and survival), mortality, immigration, and emigration.

When multiple females are pregnant simultaneously in a group, usually only the last female to give birth produces a surviving litter, because she kills the pups of females that give birth earlier (hence dominant females' tendency to evict subordinates before reproduction; see Clutton-Brock et al. 1998, 2008). As a result, pups could usually be attributed to a specific female using behavioral data. In some instances, however, multiple females produced litters almost simultaneously, and pups could not be reliably attributed to one of them. In these cases, we relied on genetic maternity assignment. Tissue samples, taken from pups upon emergence and other individuals after anaesthetization or death, were genotyped at up to 18 variable microsatellite loci (Nielsen et al. 2012). A combination of behavioral records and genetic data were used with two programs, Colony2 version 2.0.1.1 (Wang 2004) and MasterBayes version 2.47 (Hadfield et al. 2006), to infer parentage for as many members of the population as possible. When assigning maternity for individual births, any females known to have given birth in the appropriate group at the appropriate time were considered candidate mothers, and the gestational status of females, dominance status, and group membership were used as phenotypic predictors in MasterBayes. Only assignments with at least 80% individual-level confidence were considered when combining the parentage inferences from both programs to generate a categorical pedigree (Nielsen et al. 2012). If genetic information was unavailable or ambiguous for a litter, we randomly assigned pups to the candidate mothers.

We often had reliable information regarding death and dispersal; emigrants were recorded in nearby groups, carcasses were found, and predation was observed. When an individual's fate was unclear, we used knowledge of meerkat behavior (e.g., Clutton-Brock et al. 1998, 2002, Stephens et al. 2005) to assign the disappearance as either apparent emigration or apparent death. We deemed any disappearance in which an individual had shown signs of pre-dispersal in the month prior to be emigration, disappearance of a dominant individual to be death, multiple simultaneous same-sex disappearances to be group emigration, and all other disappearances to be deaths (Bateman et al. 2011*b*). Further references to death and emigration therefore refer to apparent death and apparent emigration, respectively.

To estimate population densities, we divided population-wide census counts by estimates of the population's geographic range. We estimated population range as the 95% confidence region from an empirical kernel utilization distribution (Worton 1989) fit to GPS sleeping burrow location data (collected by researchers during group visits) using a bivariate normal kernel and fixed smoothing parameter. Further details of GPS data collection and our estimation of population range are available elsewhere (see Bateman et al. 2011*a*).

We used rainfall data from the global precipitation climatology project version 2.1 combined precipitation data set (an update of the version 2 data set described in Adler et al. [2003]). Raw data were monthly rainfall estimates on a 2.5° × 2.5° (latitude × longitude) grid, which we accessed from NASA's GES-DISC (the National Aeronautics and Space Administration's Goddard Earth Sciences Data and Information Services Center) interactive online visualization and analysis infrastructure (Giovanni; NASA GES-DISC 2009).

Model overview

We extended the methods of Coulson et al. (2008), incorporating immigration and emigration in addition to natality and mortality, to model meerkat group dynamics. Broadly, this meant fitting functions to describe rates of immigration, emigration, juvenile recruitment, and mortality in discrete time windows and then combining these functions to predict group dynamics one time step, or period, at a time. Because meerkats of different age, sex, or dominance status can exhibit extreme differences in relevant demographic rates (e.g., dominant females produce almost all pups), we fit separate demographic functions for different "classes" of meerkats, considering six classes in total: dominants, immature subordinates (<1 year old), and adult subordinates (≥1 year old) for each of males and females.

We used two-month observation periods, dividing the year into six sequential pairs of consecutive calendar months (January–February, March–April, and so forth). Two months is the approximate minimum interbirth interval for meerkats, and a longer window would have introduced the potential complication of single females producing multiple litters in one time step, while too short a window would have resulted in extremely low demographic rate estimates.

For a detailed explanation of out modeling approach, see Appendix A. In short, we used generalized additive models (GAMs; Wood 2006) and information-theoretic model selection to developed maximum-parsimony descriptions of recruitment (broken into the probability of litter production, litter size, and pup survival to recruitment), mortality, immigration, and emigration rates for each stage class in relation to time of year, group size, population density, current rainfall, and rainfall in the past 10 months. We then combined the component rate models into an overall model of group dynamics to predict each group's expected size two months ahead.

Model assessment

We used R^2, the proportion of total variation in data explained by a model fit to those data, as an estimate of the explanatory ability of our final model (Coulson et al. 2008). We are aware that R^2 has its limitations, but with appropriate care R^2 provides a good measure of goodness of fit (Kvålseth 1985). See Appendix A for a detailed description of our R^2 calculations, relative to a trendless random walk model.

We also used R^2 to assess the explanatory ability of various aspects of the final model (Coulson et al. 2008). To do this, we used the relative decrease in R^2 from the full model to a reduced model, not including an aspect of interest, as an estimate of that aspects's contribution to the overall fit. In this way we assessed contributions from the five predictor variables (by refitting the model without each variable in turn); age, sex, and dominance structure (for example, to assess the effect of including sex-specific models, we estimated demographic rates for each age-by-dominance class as the weighted mean of the appropriate sex-specific rates); and each demographic rate (by fixing the predicted rate at its observed mean). To investigate potential explanations for emigration-induced declines in group size following dry years (Bateman et al. 2011*b*), we also assessed the contributions of current rainfall, past rainfall, and age-structure through emigration alone.

Simulations

To place the final model's goodness-of-fit estimate in context and to visualize overall model behavior, we adapted the predictive model into an individual-based simulation model and generated a set of 10 000 Monte Carlo simulated group trajectories. See Appendix A for further details.

Statistical software

We performed all statistical analyses and simulations in R version 2.13.1 (R Development Core Team 2011). We used the *kernelUD* function from the *adehabitat* package (Calenge 2006) to estimate kernel utilization distributions, the *gam* function from the *mgcv* package (Wood 2006) to fit GAMs, and the *optim* function (from the *stats* package) for numerical optimization.

Results

Data series

We had data from a total of 32 groups of meerkats, with between 5 and 15 (mean 11.8) groups under study at any one time. Group size ranged between 2 and 47 (mean 15.5) individuals, with periodic changes in group size somewhat synchronous, especially during major crashes in 2003 and 2007 and an apparent minor crash in 2001 (Fig. 1A). Population density ranged between 5.2 and 17.1 (mean 10.7) individuals/km^2, following the same general trends as the observed group sizes (Fig. 1A). Group density ranged between 0.5 and 0.9 (mean 0.7) groups/km^2.

The data included records for a total of 1205 individuals. There were 406 apparent deaths. 766 individuals apparently emigrated, compared to 155 individuals that joined existing groups and 105 individuals that founded new groups (including immigrants from outside the study population). There were 638 pregnancies that resulted in 343 emergent litters with a

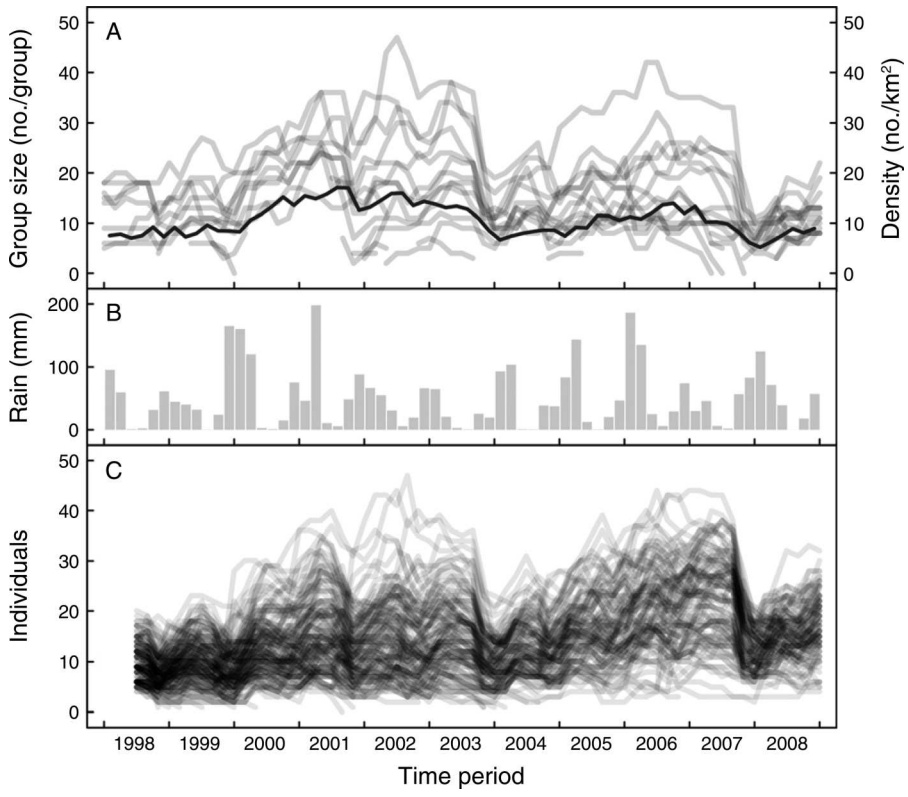

FIG. 1. (A) Observed initial meerkat group sizes (individuals/group; gray lines), meerkat study population density (individuals/km^2; black line), and (B) rainfall for two-month periods between 1 January 1998 and 1 January 2009 at the Kuruman River Reserve, South Africa. Panel (C) shows 150 group trajectories simulated from the individual-based stochastic version of a meerkat group-dynamics model. The model pseudorandomly simulated reproduction, mortality, immigration, and emigration in two-month time steps based on generalized additive model characterizations of meerkat demographic rates, parameterized using field data. Each trajectory was seeded with one of five observed group compositions from the first half of 1998.

total of 1256 pups, 1010 of which survived to recruitment age.

Rainfall was 90.4 ± 49.5 mm (mean ± standard deviation), 90.2 ± 54.4 mm, 14.7 ± 14.0 mm, 2.3 ± 2.3 mm, 29.3 ± 13.4 mm, and 70.2 ± 37.6 mm in January–February, March–April, May–June, July–August, September–October, and November–December, respectively (Fig. 1B), and 10-month rainfall averaged 203.2 ± 74.2 mm, 202.3 ± 76.6 mm, 279.7 ± 96.8 mm, 292.0 ± 100.7 mm, 264.1 ± 101.4 mm, and 227.0 ± 83.3 mm for the same periods. Rainfall reached lows in the 2002–2003 and 2006–2007 rainy seasons, just before major reductions in group size (Fig. 1B).

Component rate models

As with any modeling exercise, the design and selection of our component rate models involved trade-offs. Our aim was not to provide definitive descriptions of our system, but to identify key relationships—the most parsimonious descriptions at our disposal. We do not attempt to draw specific conclusions about the precision of individual parameter estimates; instead we discuss strong trends and take a relatively holistic view of the "best" models.

Reproduction showed two main trends: subordinate females reproduced far less than dominants (Appendix B: Table B1; Fig. 2), mainly due to a lack of litter production rather than reduced litter size or pup survival, and reproduction was severely reduced in dry years (Fig. 3; Appendix B: Figs. B7–B10), again due to reductions in litter production. Litter production generally peaked in January and reached a low in July but increased with short-term rainfall and occurred throughout the year if conditions were wet (Appendix B: Figs. B7–B10); litter production all but ceased in off-peak months when conditions were dry, but dominants tended to produce January litters regardless of rain (Appendix B: Fig. B7). Extremes in ten months' total rainfall reduced the probability of litter production, with dry conditions in the 10 months prior to July particularly detrimental (Appendix B: Figs. B7, B8). Dominant females produced more litters in large groups, while the reverse was true (per capita) for subordinates (Appendix B: Figs. B7, B8). The mean litter sizes (for litters of at least one emergent pup) were 3.82 pups for dominants and 3.29 pups for subordinates. Pup survival for dominant female litters peaked around January in slightly wetter-than-average conditions (both just after

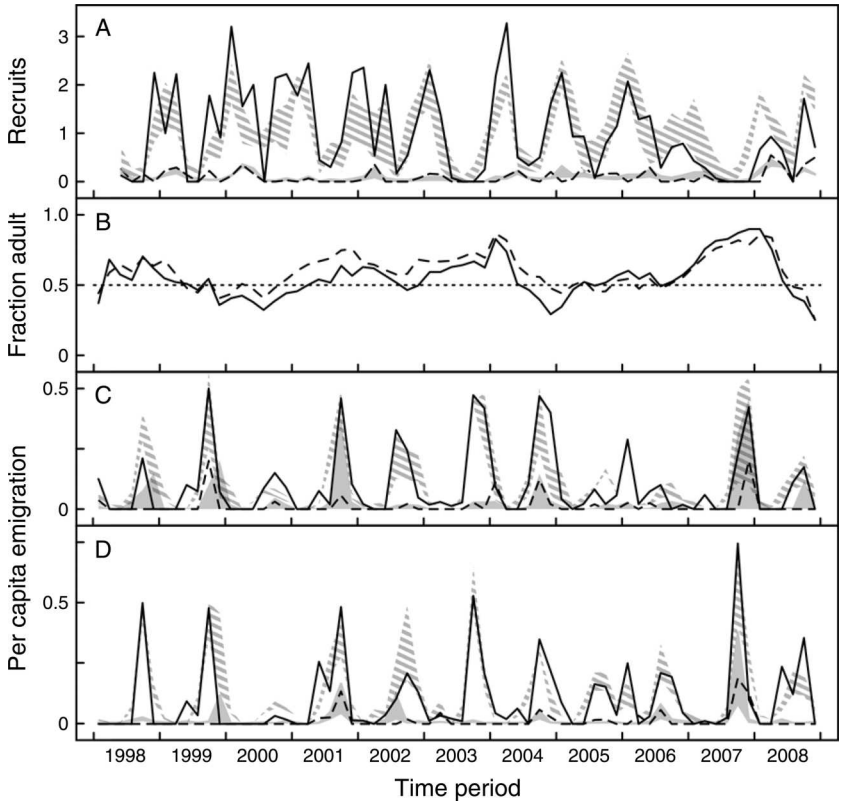

FIG. 2. Factors effecting crashes in meerkat group sizes. (A) Reduced rates of reproduction in dominant females (solid line) after relatively dry rainy seasons (reproduction in subordinates [dashed line] is consistently low) contribute to (B) adult-biased age structure in subordinate females (solid line) and males (dashed line). This combines with patterns of emigration in (C) subordinate females and (D) males (emigration rates are much higher in adults [solid lines] than in immature individuals [dashed lines] and increase following dry conditions) to bring about large emigration events. Hatched and solid gray regions show the ranges, across observed group sizes, of mean model predictions corresponding to solid and dashed population-mean observations, respectively.

birth and in the preceding 10 months), while pup survival for subordinate litters benefited from increased rainfall in the relevant period and varied little with season. All pups were most likely to reach recruitment age in groups of slightly more than 20 individuals (Appendix B: Figs. B9, B10).

Rates of within-group mortality were very low (Fig. 3). For most classes, mortality was highest in the dry season, but dominant males also tended to die in the wet season if conditions in the previous 10 months had been dry, and seasonal effects were less apparent in females (Appendix B: Figs. B1–B6). The effects of rain and population density varied across demographic classes, but individuals in larger groups consistently enjoyed reduced mortality (Appendix B: Figs. B1–B6).

Rates of emigration generally peaked between July and September, and were much higher for subordinate adults than for other meerkat classes (Fig. 2; Appendix B: Table B1, Figs. B11–B15). For adult subordinates, emigration was similar for both sexes, tending to occur most in September from large groups when conditions had been dry in the past 10 months or when conditions were relatively wet (Appendix B: Figs. B13, B15). For adult subordinate females, however, emigration was rare in wet conditions after the past 10 months had been dry and at high population densities.

Male-only immigration into established groups also peaked between July and September, but increased with rain in a given period and was highest when rain in the previous 10 months was slightly above average (Appendix B: Fig. B16). Absolute rates of immigration declined initially with group size, reaching a minimum for groups of just over 20 individuals, and increasing thereafter; however, the equivalent per capita rates of immigration were maximized in small groups and remained consistently low for groups of >10 individuals (Appendix B: Fig. B16). The negative binomial shape parameter for the distribution of immigration in a given period was 0.086, producing a heavily right-skewed distribution with mode at 0.

Rates of recruitment and immigration showed higher levels of stochastic noise, relative to mean model predictions, than did rates of mortality and, in particular, emigration. For immigration, this was due to the considerable aggregation, but rarity, of the process. For recruitment, it was due to the fact that a

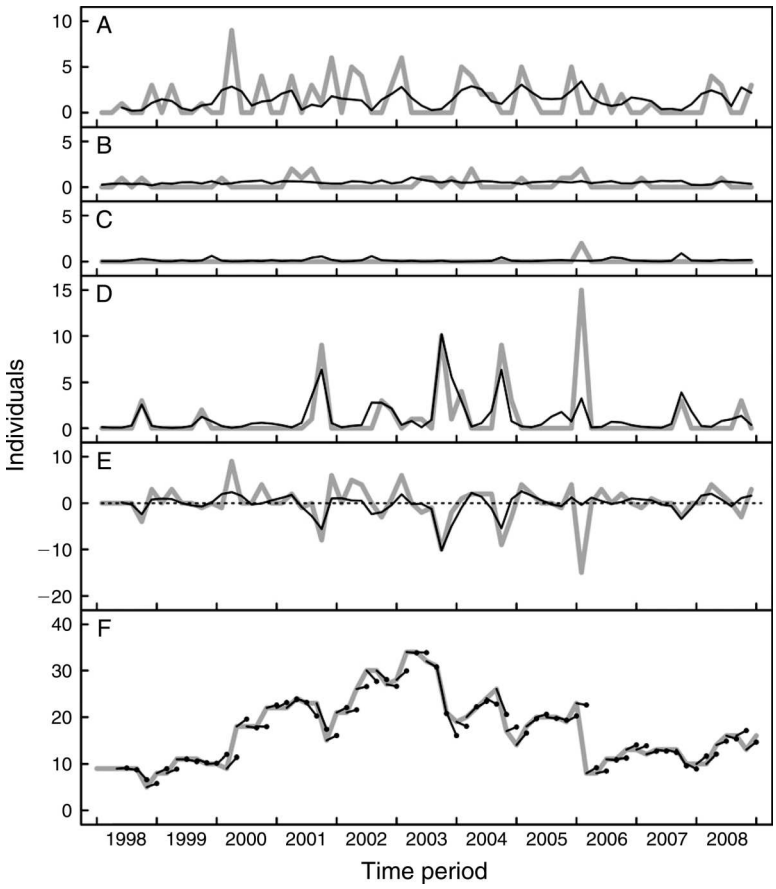

FIG. 3. Demography of a single meerkat group between 1 January 1998 and 1 January 2009. Lines show observations (gray) and generalized additive model expectations (black) for (A) recruitment, (B) mortality, (C) immigration, and (D) emigration during two-month periods. The resultant (E) changes in group size relate (F) group size at the start of each period to group size at the start of the next period (i.e., time step; the model relates each group size observation to a single subsequent prediction). All units are the number of individuals.

single dominant female, either breeding or not breeding, was responsible for most reproduction within each group; reproductive models combined to predict intermediate but sustained levels of recruitment throughout the breeding season, but large litters produced an abundance of pups while failures to breed produced none, and both were common (Fig. 3). On the other hand, emigration tended to occur in more concentrated bursts across more individuals, leading to less stochasticity on average (Fig. 3).

Crash dynamics

The abrupt decreases in group size seen in "crash" years (Fig. 1A, C) were due to a combination of recruitment and emigration processes, partially mediated by changes in group composition. Three factors—current rainfall, past rainfall, and changes in age structure—contributed substantially to the model's ability to describe these environment-dependent patterns of emigration (10%, 14%, and 9%, respectively, overall contributions to the models explanatory ability; Appendix B: Table B2). Litter production all but ceased in dry conditions (except at the peak of the breeding season; Appendix B: Fig. B7), and recruitment, especially in the periods surrounding the usual July–August low season, therefore suffered after dry years (Fig. 2A). Emigration also fell during the usual season in dry years (Appendix B: Figs. B13, B15). These effects led to an increase in the ratio of adult to immature subordinates in the following emigration season (Fig. 2B). Per capita emigration rates were elevated after low-rainfall years, and the emigration rates of adult subordinates were much higher than those of immature subordinates (Fig. 2C, D). When paired with the changes in subordinate age structure, this led to sharp declines in group size.

Predictive model

Combining the component rate models into an overall model to predict each group's expected size two months ahead explained ~40% of the observed variation in group size (Appendix B: Table B2). Of the explanatory variables considered, seasonality accounted for 60% of the model's overall explanatory ability, current and past rain each accounted for 15%, and group size, followed

by population density, accounted for most of the rest (Appendix B: Table B2). Taken together, demographic structure (allowing for different demographic rates across meerkat classes) accounted for almost 30% of the model's explanatory ability, with dominance structure responsible for the most (Appendix B: Table B2). Of the various demographic rate models, those of emigration accounted for two thirds of the explanatory ability of the overall model, with those of reproduction (and in particular of the probability of litter production) accounting for almost one fifth of the overall explanatory ability; immigration and mortality models accounted for relatively little (Appendix B: Table B2).

Individual-based simulations

As a set, the individual-based simulations of group dynamics captured observed patterns well (Fig. 1C). Simulated dynamics corresponded with observed annual patterns and past models of annual dynamics; in particular, the simulations reproduced the major crashes in 2003 and 2007, as well as the minor crash in 2001, and the intervening periods of growth and relative stability (Fig. 1C; Appendix B: Figs. B17, B18; Bateman et al. 2011*b*). Simulated groups also generally displayed appropriate patterns of seasonal growth and decline, tending to grow moderately from January through June and crash or remain relatively static (depending on year) from July through December (Appendix B: Fig. B17). Model fits for empirical group trajectories were statistically similar to model fits for model-simulated trajectories (Appendix B: Fig. B19).

Discussion

Our model shows that meerkat group-size dynamics are governed primarily by reproduction and emigration. On average, groups increase moderately between January and July (Appendix B: Fig. B17A) due mainly to production of recruits by the dominant female. From July to January recruits are produced at lower numbers, and group size tends to decrease (Appendix B: Fig. B17B) as a result of emigration, especially in large groups if the past rainy season was relatively dry. This model provides detail at a much finer temporal resolution than past models (Bateman et al. 2011*b*) and allows us to investigate the role of social structure on group dynamics.

In particular, our model provides detail surrounding the social and environmental mechanisms behind declines in group size following low-rainfall years. Sharp declines in the size of large groups after dry rainy seasons are due partially to the effect of rain on stage-specific dispersal rates, but also to rainfall's effects on reproduction, subsequent shifts towards older age structure, and differences in age-dependent dispersal rates. Reduced rates of reproduction in dry years lead to relative declines of non-dispersive immature individuals within groups, and, as a result, group-wide per capita rates of emigration increase in the following dispersal seasons. Thus, although we can attribute less of our model's short-term explanatory ability to recruitment than to emigration (Appendix B: Table B2), we see that the former is integral in explaining trends in group dynamics, and the model's realistic simulated dynamics over the longer term support this.

Past work was only able to identify elevated average emigration rates after dry years (Bateman et al. 2011*b*), leaving the question of mechanism entirely unanswered. Rather than ruling out one of the potential explanations for group-size declines following dry years (Bateman et al. 2011*b*), our model reveals a system in which demographic shifts and rain-related changes in behavior both appear to be important.

Model performance

The model provided a good description of dynamics in a socially complex and environmentally variable system. The component rate models described the major contributing rates (recruitment and emigration) well at the population level (Fig. 2), and emigration predictions closely matched observations at the group level, but recruitment within each group proved more difficult to capture (Fig. 3). Because most reproductive events produced multiple recruits, small errors in predicting litter production led to larger errors in predicting the number of recruits in any period. Nevertheless, the overall model's predictions matched observed patterns of change (e.g., Fig. 3E) and explained $>40\%$ of the observed variation in group size.

Individual-based simulation confirmed the ability of the model to match observed patterns over longer timescales. Simulated group dynamics qualitatively matched observed group dynamics (Fig. 1C; Appendix B: Figs. B17, B18), with year-by-year patterns in the set of simulated trajectories matching those from the set of real groups, including group-size crashes after particularly low-rainfall years (compare Fig. 1A and C). The simulations also provided a description of average annual dynamics in relation to past rainfall that is very similar to that provided by classical phenomenological population dynamics models (compare Appendix B: Fig. B18 to Figs. 1 and 4 in Bateman et al. 2011*b*).

We note that, because of our constrained definition of a group (at least one female present), we were forced to abandon simulated groups that became all male. This mirrors practice in the field, but does not explicitly account for the formation of what are, in effect, large cohorts of male dispersers. Something similar holds for all-female groups, which we did follow in our simulations, but which effectively represent large cohorts of female dispersers.

Group-level implications

Group size plays an important role in the frequency with which dominant females evict subordinates and the frequency with which subordinates disperse. Though the

likelihood that a dominant female reproduces increases with group size, it increases little once her group surpasses 30 individuals, and the survival prospects of her pups appear to suffer in large groups (Appendix B: Fig. B7; Hodge et al. 2008). Large groups are also more likely to produce large cohorts of emigrant females, which are better able to form new groups (Young 2003). Thus, although female group membership is thought to be largely under dominant control, it appears to be in the interests of both dominants and subordinates that emigration should increase in larger groups (Young 2003, Stephens et al. 2005), and the propensity of subordinate females to emigrate could explain paradoxically low rates of challenges to the status of dominant females (Sharp and Clutton-Brock 2011).

High rainfall in a given period and low rainfall in the preceding 10 months are both associated with relatively high rates of subordinate emigration in both sexes. The former corresponds to favorable current conditions while the latter is associated with poor physical condition in meerkats (English et al. 2011). Females disperse either to establish new groups or because they fail to return to their group after being forced out by the dominant female, in her effort to avoid reproductive conflict and infanticide (Clutton-Brock et al. 1998, 2008, Stephens et al. 2005). Notably, female emigration is reduced in dry years, at precisely the same time that dominant litter production suffers and reproductive conflict is thus at a minimum (Clutton-Brock et al. 1998, 2010). Males disperse to establish new groups and to find extra-group mating opportunities (Doolan and Macdonald 1996, Young 2003). Both eviction for females and prospecting for males are physiologically costly, stressful events (Young 2003, Young et al. 2006, Young and Monfort 2009). While favorable environmental conditions are likely to give rise to group-formation attempts, poor physical condition, combined with high levels of physiological stress, is likely to be associated with elevated extra-group mortality rates that show up here as increased rates of apparent emigration. The lack of apparent adult-subordinate-female emigration in wet conditions after dry periods could be due to those females being in too poor a condition to emigrate successfully but having access to sufficient resources to avoid eviction-related mortality.

Our approach was good at predicting the timing and population-wide mean levels of male-only immigration but unable to accurately predict group-specific immigration. Occasionally, when immigrant males expelled resident males, this led to errors in the prediction of emigration as well (e.g., Fig. 3D). Our inability to precisely predict immigration was largely due to the fact that male immigration is rare and clustered (i.e., males tend to immigrate in groups). Future attempts to investigate the effects of immigration may, therefore, be best served by simulation-based approaches in place of assessment of mean rates.

Population-level implications

Although we did not explicitly consider population-level dynamics in our model, they appear to be closely tied to group-level dynamics (Fig. 1A), and population density closely parallels median group size. If this pattern persists beyond our study population, it would suggest that group territories, in size at least, are relatively stable, and that the population-level response to favorable conditions is largely an increase in density through group augmentation. Aggressive interactions between meerkat groups are common, with large groups often chasing smaller groups out of their range (Young 2003), and this probably hinders new group formation under otherwise favorable conditions. High population density does appear to inhibit adult subordinate female emigration; in a saturated local environment, group-establishment prospects would be limited, and dispersal would provide little benefit at high cost.

Group turnover does occur, however, and few of the groups we followed were present for the duration of the study. Some moved out of the study area, but others disbanded or died out. Not surprisingly, the few groups we observed to collapse entirely were small (although this appears to be due to stochasticity rather than inverse density dependence [Allee effects]; Bateman et al. 2011*b*), and their collapses generally coincided with low-rainfall years or emigration-mediated declines in group size (Fig. 1; Appendix B: Fig. B18).

As large emigration events directly precede the rainy season, group formation resulting from dispersal would be well timed to take advantage of favorable conditions. After crash years, newly formed groups might be better able to compete with reduced existing groups or take over territory from groups that perished, and this might contribute to increased rates of apparent emigration after dry years. It also suggests that dispersal in poor years, even if it puts some groups at risk, may facilitate population recovery after periods of decline.

Although not strictly equivalent, the meerkat system resembles a metapopulation and, given the patterns of demography and dispersal, presents the potential for source–sink dynamics (Hanski 1999). Large groups appear to act as sources, their emigrants able to augment other groups and colonize empty habitat patches or regions of marginal habitat (collectively, sinks). These sinks, in turn, could have an important stabilizing effect on the population of source groups, which are both intrinsically stochastic and susceptible to extrinsic environmental stochasticity (Hanski 1999). Given the location of our study population, in what seems to be meerkats' preferred territory (along a dry riverbed; Clutton-Brock et al. 1999*b*) surrounded by marginal habitat, the potential for interesting local and regional source–sink dynamics certainly exists.

Male dispersal behavior has the potential to strongly affect population dynamics. Because resident males are sometimes forced to emigrate when foreign-group males move in, single dispersal events potentially generate

effects population wide. Immigration events appear to be able to spur even larger, otherwise unpredicted emigration events (e.g., Fig. 3C, D). Groups thus reduced in size might be less able to defend territories, shifting otherwise stable patterns. Pre-dispersal behavior may also affect population dynamics: past work indicates that group interactions may drive male prospecting behavior and affect disease transmission (Doolan and Macdonald 1996, Drewe et al. 2009).

Broader implications

For meerkats, environmental fluctuations alter stage structure across groups, contributing the observed dynamical patterns. Past work has shown that differentially stage-structured populations of the same size can respond differently under identical conditions (Coulson et al. 2001) and that stage structure has implications for the dynamics of disease, invasion, and at-risk populations (Fulford et al. 2002, Koons et al. 2005, Miller and Tenhumberg 2010). There is growing consensus that investigations of stage-structured populations relying on characterizations of asymptotic dynamics provide limited insight into the behavior of those populations under conditions of interest (Koons et al. 2005, Ozgul et al. 2009, Miller and Tenhumberg 2010).

Spatial and social structure add complexity to the investigation of population dynamics and can affect population responses to given sets of conditions (Packer et al. 2005, Ozgul et al. 2009). Local processes combine to produce population-wide patterns, but the relationships are not always simple, and when local conditions affect per capita demography, observed dynamics can differ markedly from population mean predictions (Morales et al. 2010). Even in relatively simple systems, large-scale dynamics can be difficult to explain based on local dynamics (Hanski and Meyke 2005). Here, however, we have a socially complex species for which observed group dynamics, though exhibiting stochastic noise, are closely correlated and match patterns of change in local population density (although population density seems to decline slightly just before sharp declines in group size; Fig. 1A).

Conclusion

By considering the effects of social and environmental factors on contributions to group dynamics at fine temporal resolution, we were able to describe the mechanisms by which environmental conditions control group size in meerkats. Climate variation influences dispersal behavior and leads to changes in groups' demographic structure, producing lagged changes in group size. Our detection of this mechanism relied on an integrated modeling approach that considered stage-structured demography at a fine timescale.

Population dynamics in socially structured populations are the result of both within-group and among-group processes. In reality, the two processes are intimately tied to one another, and in order to improve our understanding of spatially structured population dynamics we must work towards integrated models that consider both in concert (Bowler and Benton 2005). The dispersal-related processes that we identified as important to meerkat group dynamics are also the processes that have the largest potential effect on population-level dynamics, and future work will focus on the connections among group dynamics, inter-group movement, group formation, and population-level dynamics.

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Supplemental Material

Appendix A

Details of model formulation and assessment (*Ecological Archives* E094-051-A1).

Appendix B

Details of final model, component-rate submodels, and model simulations (*Ecological Archives* E094-051-A2).